

DESCRIPTION OF A PAEDOPHAGOUS DEEP-WATER CICHLID (TELEOSTEI: CICHLIDAE) FROM LAKE MALAWI, AFRICA

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Abstract.—A deep-water paedophagous cichlid of the genus *Diplotaxodon* is described from Lake Malawi, Africa. Similarity of jaw morphology between this species and shallow-water paedophages which obtain eggs and larvae by ramming brooding females, suggest that this deep-water cichlid obtains food in the same manner.

The exploitation of fish eggs, embryos, and larvae (i.e., paedophagy) was first reported for haplochromine fishes by Greenwood (1959, 1967, 1974). Recent studies of the shallow water fauna of Lake Malawi led to the discovery of a group of three fish species which specialized in ramming females to take young from their mouths (McKaye and Kocher 1983). This ramming mode of feeding was suggested, contrary to hypotheses from earlier studies (Greenwood 1959, Fryer and Iles 1972, Wilhelm 1980), to be one of the general methods by which paedophagous cichlids gathered their prey in the lakes of Africa. The other method is to steal eggs after they are laid, but before the female can gather them into her mouth, as done by *Cyrtocara ovatus*, *Cyrtocara insignis*, and *Cyrtocara labifer* (McKaye 1984).

Deep water trawls in Lake Malawi produced four specimens of an undescribed species of *Diplotaxodon*, one of which had cichlid eggs in its stomach. The purpose of this paper is to describe this deep-water paedophage. External counts and measurements follow Barel et al. (1977).

Diplotaxodon greenwoodi, new species
Fig. 1

Holotype.—National Museum of Natural History (USNM) 270847, adult female (ripe)

(Fig. 1), 198.7 mm standard length (SL), 8 km south of Mumbo Island, 34°45'E, 14°04'S, Cape Maclear, Lake Malawi, at 86 m. Collected by KRM and JRS, Field Collection Number JRS-84-29, 17 Apr 1984.

Paratypes.—USNM 270848 (3 specimens, females, 167.2 (ripe) 111.9 (immature), 140.3 (immature) mm SL), same data as holotype.

Description.—This description is based upon the holotype and 3 paratypes. Principal morphometric ratios and meristics are presented in Table 1.

Body form.—The body is moderately compressed. Body depth ranges between 342–365 thousandths of standard length. Distances between snout and dorsal fin origin and snout and pelvic fin origin range between 382–404 and 452–472 thousandths of standard length, respectively. The holotype had 16 abdominal vertebrae and 18 caudal vertebrae. The three paratypes had 16 + 17, 15 + 17, and 15 + 18 abdominal and caudal vertebrae (counts from radiographs).

Head.—Head length ranges between 374–381 thousandths of SL. The eye is large (horizontal eye diameter, 275–354 thousandths of HL). There are either two or three scale rows on the cheek. The jaw is prognathous and the gape inclination ranges between 57–66 degrees. The mean length of the lower jaw is 487 thousandths of HL.

Table 1.—Principal morphometric and meristic characteristics of *Diplotaxodon greenwoodi* (n = 4 and includes holotype).

	Holotype	Mean	Range	SD
Standard length, mm	198.7	154.5	111.9–198.7	37.1
Head length, mm	75.1	58.3	42.1–75.1	14.2
Thousandths of HL				
Horizontal eye diameter	275	309	276–354	34
Vertical eye diameter	278	310	278–352	33
Snout length	317	299	242–342	43
Postorbital head length	406	389	380–406	12
Premaxillary pedicel	173	191	173–200	13
Lower jaw length	519	487	460–519	25
Interorbital width	189	176	166–193	18
Cheek depth	217	185	159–201	28
Head depth	870	850	824–870	21
Thousandths of SL				
Head length	378	377	374–381	3
Snout to dorsal	383	396	383–404	10
Snout to pelvic	453	459	453–472	9
Body depth	355	354	342–365	9
Least caudal peduncle length	196	185	168–196	14
Least caudal peduncle depth	113	112	109–115	3
Pectoral fin length	329	320	306–332	13
Pelvic fin length	199	198	180–210	13
Dorsal fin base length	459	447	426–459	15
Gape inclination (degrees)	63	62.3	57–66	3.8
Lateral line scales	34	34	34	—
Scale rows on cheek	2	2.5	2–3	0.58
Pectoral fin rays	13	12.5	12–13	0.58
Pelvic fin rays	5	5	5	—
Anal fin spines	3	3	3	—
Anal fin rays	10	10.3	10–11	0.5
Gill rakers on ceratobranchial	20	19.3	19–20	0.5
Gill rakers on epibranchial	6	5.3	5–6	0.5

There is a small ventral protrusion present at the symphysis of the dentaries.

Teeth on the lower jaw of the holotype are in three rows, while those on the upper jaw are in four rows. Teeth in fourth row do not extend as far posteriorly as the others. All teeth are unicuspid. Those on the lower jaw are embedded in the soft tissue of the jaws.

Gill rakers are single filaments and on the ceratobranchial range in number between 19–20. There are 6 on the epibranchial, with one in the angle between the ceratobranchial and epibranchial bones.

Fins.—Mean dorsal fin base length is 447 (426–459) thousandths of standard length. Pectoral fins are comprised of 12–13 segmented rays. Anal fins have three spines and 10–11 segmented rays.

Lower pharyngeal bone.—The lower pharyngeal bone was dissected from the holotype. It is triangular in outline with two tooth forms (Fig. 1). Both tooth forms are conical, with those on the posterior part of the bone straight, while those laterally are slightly recurved.

Squamation.—Scales are ctenoid, with 34 pored lateral line scales. Scales uniformly

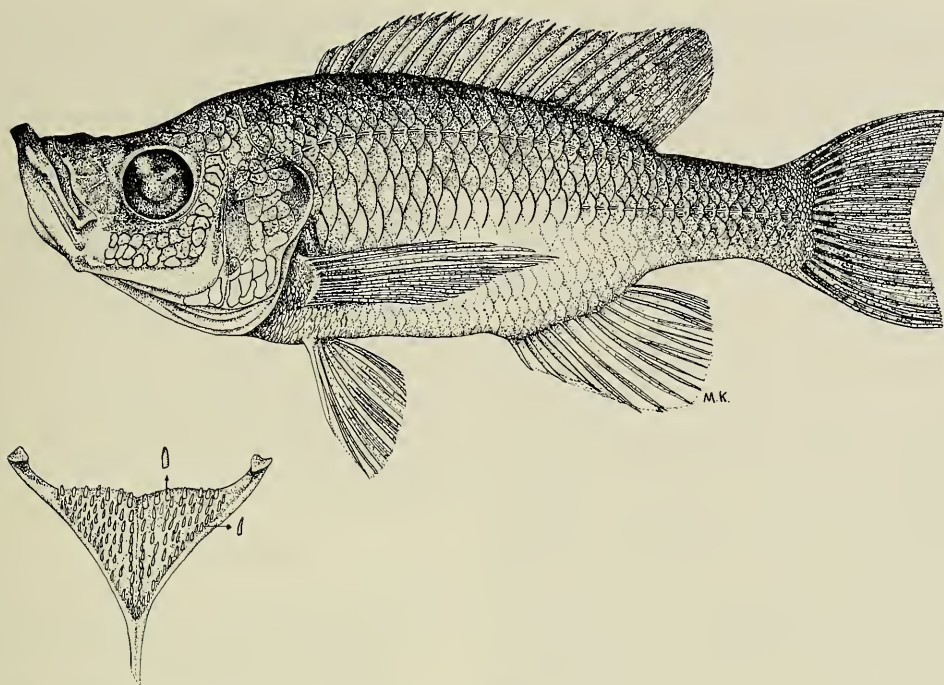


Fig. 1. Holotype (USNM 270847) of *Diplotaxodon greenwoodi*.

cover the anterior third of the caudal fin, partially cover the middle third, and are essentially absent from the posterior third.

Coloration.—Freshly collected specimens are dark dorsally, with a purple sheen. The lateral surfaces are silver, but fade to white ventrally.

Diagnosis.—Trewavas (1935:68) distinguished the genus *Diplotaxodon* as follows: “third, or third and fourth vertebrae with inferior apophyses which are short, and do not approach each other below dorsal aorta; vertebra 16 + 18; teeth conical, in two series; premaxillaries not beak-like.” *Diplotaxodon greenwoodi* differs from the other two described species in the genus, *D. argenteus* and *D. eccelsi*, by the increase in gape inclination, and vertebral number. There is also a fourth row of teeth on the upper jaw. An analysis of the phylogenetic relationships of *D. greenwoodi* must await revision of the genus, which probably con-

tains some 20 undescribed species (Iles, pers. comm.).

Discussion.—Most specimens trawled from below 70 meters had completely everted guts when they reached the surface. However, the gut of the holotype contained eggs, which were identical in shape and size with those contained in the ovaries of *Lethrinops gossei* which were collected simultaneously. It is conceivable that the eggs in the stomach of *D. greenwoodi* were a result of “trawl snatching.” However, the presence of numerous ripe male and female *L. gossei* in the trawl sample indicates that the trawl was made over an *L. gossei* breeding arena where the presence of a paedophage would be expected. That the paedophage was relatively rare (< 0.1% of cichlids caught in trawl) is consistent with data collected on shallow-water paedophages (Fryer and Iles 1972, McKaye and Kocher 1983).

The feeding behavior of *D. greenwoodi*

has not yet been observed because it occurs at depths below our present diving capabilities. Nevertheless we hypothesize that *D. greenwoodi* is a paedophage which obtains eggs and larvae by ramming brooding females, in a manner convergent with that in *Cyrtocara orthognathus* and *Cyrtocara liemi* (McKaye and Kocher 1983). This behavioral hypothesis is inferred from the morphology of *D. greenwoodi*. The head shape, particularly gape inclination (ranging between 57–66 degrees), closely resembles that of *C. orthognathus* and *C. liemi*, which are known ramming paedophages (McKaye and Kocher 1983). Examination of the gape inclination of the holotype (USNM 227497), and two paratypes (USNM 227501; 227503) of *C. liemi* showed that the gape inclination ranged between 41–45 degrees. Gape inclination of three specimens of *C. orthognathus* (British Museum Natural History [BMNH] 1973.3.26:88; 1956.6.4:4; 1969.3.11:17) ranged between 67–74 degrees. Both *C. liemi* and *C. orthognathus* obtain eggs and larvae by stalking brooding females in the water column, and approaching these females from underneath and behind before ramming them.

Convergence in form among paedophages is further supported by *D. greenwoodi* dentition. Teeth are restricted to the anterolateral parts of the upper and lower jaw bones and are buried in a thickened oral mucosa. A similar condition exists in both Lake Victoria haplochromine lineages of paedophagous fishes which are now placed in the genus *Lipochromis* and given subgeneric rank of *Lipochromis* and *Cleptochromis* (Greenwood 1979).

Etymology.—Named after P. H. Greenwood in recognition of his renowned studies of cichlid fishes, and for being the first to discover this unique feeding specialization in cichlids.

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Literature Cited

- Barel, C. D. N., M. J. P. van Oijen, F. Witte, and E. L. M. Witte-Mass. 1977. An introduction to the taxonomy and morphology of the haplochromine Cichlidae from Lake Victoria.—*Netherland Journal of Zoology* 27(4):339–389.
- Fryer, G., and T. D. Iles. 1972. The cichlid fishes of the Great Lakes of Africa. Edinburgh: Oliver & Boyd, 641 pp.
- Greenwood, P. H. 1959. A revision of the Lake Victoria *Haplochromis* species (Pisces, Cichlidae), Part 3.—*Bulletin British Museum of Natural History (Zoology)* 5:179–218.
- . 1967. A revision of the Lake Victoria *Haplochromis* species (Pisces, Cichlidae), Part 6.—*Bulletin British Museum of Natural History (Zoology)* 25:139–242.
- . 1974. The cichlid fishes of Lake Victoria, East Africa: The biology and evolution of a species flock.—*Bulletin British Museum of Natural History (Zoology) Supplement* 6:1–134.
- . 1979. Towards a phyletic classification of the 'genus' *Haplochromis* (Pisces, Cichlidae) and related taxa. Part II; the species from Lakes Victoria, Nabugabo, Edward, George and Kivu.—*Bulletin British Museum of Natural History (Zoology)* 39:1–101.
- Mayr, E. 1963. Animal species and evolution. Harvard University Press. Cambridge, Massachusetts. 797 pp.
- McKaye, K. R. 1984. Behavioural aspects of cichlid reproductive strategies: Patterns of territoriality and brood defence in Central American substratum spawners versus African mouth brooders. Pp. 425–273. *In* R. J. Wootton and G. W. Potts (eds.) *Fish reproduction: Strategies and tactics*. Academic Press, London.

- , and T. Kocher. 1983. Head ramming behavior by three paedophagous cichlids in Lake Malawi, Africa.—*Animal Behavior* 31:206–210.
- , and C. Mackenzie. 1982. *Cyrtocara liemi*, a previously undescribed paedophagous cichlid fish (Teleostei: Cichlidae) from Lake Malawi, Africa.—*Proceedings of the Biological Society of Washington* 95:398–402.
- Trewavas, E. 1935. A synopsis of the cichlid fishes of Lake Nyasa.—*Annals and Magazine of Natural History* 10(7):133–152.
- Wilhelm, W. 1980. The disputed feeding behaviour of a paedophagous Haplochromine cichlid (Pisces) observed and discussed.—*Behaviour* 17: 310–323.
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